

ABSTRACTS OF PAPERS

Ninth Annual Albert L. Tester Memorial Symposium 12–13 April 1984¹

The Albert L. Tester Memorial Symposium is held in honor of Professor Albert L. Tester who, at the time of his death in 1974, was Senior Professor of Zoology at the University of Hawaii. The faculty and students of the Department of Zoology proposed an annual symposium of student research papers as a means of honoring, in a continuing and active way, Dr. Tester's lively encouragement of student research in a broad range of fields in marine biology. Papers reporting original research on any aspect of biology are solicited from students at the University and these papers are presented at the symposium, which takes place during the spring semester. Income from contributions to the Albert L. Tester Memorial Fund of the University of Hawaii Foundation is used to provide two prizes for the best papers by graduate students. Papers are judged on quality, originality, and importance of research reported, as well as the quality of the public presentation. Judges include several members of the faculty of the Department of Zoology as well as winners of the symposium from the preceding year, when possible. In addition, a distinguished scholar from another university is invited to participate in the symposium as a judge and to present the major symposium address. This year Joseph Connell of the University of California, Santa Barbara, participated in the symposium.

Seasonal Contrasts in the Social Behavior of the North Pacific Humpback Whale

C. SCOTT BAKER²

The long-range migration and seasonal changes in the motivational regimes of baleen whales provide an opportunity for unique behavioral strategies to evolve. Studies of the humpback whale in Hawaii and Southeast Alaska have revealed profound seasonal differences in the social organization and behavior of the humpback whale. The social organization of humpback whales in Hawaii

can be described as a polygamous mating system involving male–male competition for sexually mature females. Agonistic behavior is common and pod composition is very fluid. Whales move rapidly through island regions and exhibit little site-fidelity. The social organization of humpback whales in Southeast Alaska is characterized by noncompetitive and, at times, cooperative feeding behavior. Individual whales are often associated for several months and site-fidelity is common. Long-term associations between individuals across several seasons have been documented.

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Statoliths as Age Indicators in Gastropod Larvae: Application to Measurement of Field Growth Rates³

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Many questions concerning growth and metamorphosis in invertebrate larvae remain unanswered due to the lack of accurate age information from wild populations. For gastropod larvae, the statolith, an integral part of the sensory apparatus of the statocyst, may provide age estimates. The statoliths of prosobranch and opisthobranch larvae, when dissected, mounted, and viewed with light microscopy, displayed incremental patterns. Statoliths from laboratory cultured *Littorina scabra* demonstrated a one-to-one correspondence between increment number and age in days after release from the female. Furthermore, as increment number increased, the statolith grew in size. Larvae fed every other day demonstrated the same daily increments as those fed every day. In addition, increments were indistinguishable or nonexistent in the statoliths of larvae reared in constant light or

constant darkness, but visible in those reared on a 12:12 LD cycle. This suggests that daily changes in light may cause the alterations in deposition of statolith material which are visible as layers. Deposition of layers in the statolith was not influenced by feeding periods, but may be a response to a daily stimulus, possibly the light-dark cycle. Statoliths can now be used to assess field growth rates with some confidence that increments are deposited daily and not in response to discrete feeding episodes. To demonstrate this, plankton tows were taken to collect the larvae of *Serpulorbis variabilis*, which are easily distinguished from other gastropod larvae. The number of layers in the statoliths was correlated with larval shell length. If the layers represent age, and given a sufficient number of the largest larvae, it may be possible to estimate the timing of metamorphosis.

Tissue Water Relations of Bog and Rainforest Plants of Alakai Swamp, Kauai, Hawaii⁵

JOAN E. CANFIELD⁶

Functional responses of two pair of endemic Hawaiian plant taxa from montane bogs were compared to help explain their differential distributions. *Metrosideros polymorpha* var. *incana*⁷ (Myrtaceae) is nearly

limited to open bogs; *M. p.* var. *glabrifolia* is largely limited to the surrounding rainforest. *Dubautia paleata* (Compositae) is largely limited to open bogs, while *D. raillardoides* is restricted entirely to the rainforest. Tissue water status was determined by field measurement of diurnal water potential, using a pressure chamber. Tissue osmotic properties were determined by the pressure-volume technique, which involves repeated determination of tissue water potential and relative water content as branches are dehydrated beyond the point of zero turgor.

The midday water potential of plants growing in the bog was found to be more negative than that of the same taxon growing in the

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⁷Epithets of *Metrosideros* are used provisionally.

rainforest. Plants growing in bogs must therefore be subject to greater internal water deficits than those growing in rainforest. Pressure-volume curves indicate that tissue osmotic potential at full turgor is more negative in taxa typically limited to bogs than in taxa limited to the rainforest. Because of their greater maximum turgor, taxa limited to bogs can maintain a higher turgor pressure as tissue

water content and tissue water potential decrease. Since many physiological processes are recognized to depend closely on tissue turgor pressure, the osmotic properties of the bog taxa (*M. p.* var. *incana* and *D. paleata*) should promote their growth in the bog habitat. Properties of tissue water relations may thus contribute to the development and maintenance of the distinctive flora of Hawaiian bogs.

New Findings on the Systematics, Cytology, and Reproductive Strategies of *Porphyra* (Bangiaceae, Rhodophyta) in Hawaii and California

MARILYN I. CANNON⁸

In Hawaii, *Porphyra* species are a "folk seaweed" and have been eaten for centuries as *limu lu'au* by native Hawaiians, but there has been no species identification nor previous biological investigation of the annual winter-spring *Porphyra* species. Primarily a temperate-water genus, these annual *Porphyra* species are the only members of the genus known to occur in the Hawaiian Islands. As an economically important seaweed in Japan and China, there is considerable interest in the fact that *Porphyra* species occur in the central and eastern Pacific Ocean. The Hawaiian *Porphyra* species are compared in this study to newly discovered *Porphyra* species from the California coast.

Collections and observations of *Porphyra* populations were made throughout the year in northern California and during the winter-spring season on Oahu. Freshly collected living specimens were studied and photographed using light microscopy, and portions were fixed for cytological study with transmission electron microscopy and scanning electron microscopy. Monospores and carpospores from various *Porphyra* species were cultured in the laboratory, producing foliose blades and "Conchocelis" filaments, respectively. Herbarium specimens were prepared for all species.

Seven species new to California were dis-

covered during the course of this research. Two *Porphyra* species new to Hawaii are also reported. Three species, *P. lanceolata* (Setch. & Hus) Smith, *P. pseudolanceolata* Krishn., and *P. maculosa* Conway were discovered to have a monospore cycle, an asexual mode of reproduction. The uneven division of cells into monospores implies a closer relationship with the family Erythropeltidaceae than has been previously realized; formerly, this family was distinguished from the Bangiaceae by unequal cell division. Another discovery was the cell cycle division patterns and diurnal cycle of carpospore development. The Hawaiian species of *Porphyra* have characteristics that delineate them from those that occur in California, but also produce "Conchocelis" phases, as do California and other *Porphyra* species.

There are more *Porphyra* species along the coast of California than previously recognized; two new species native to Hawaii also have distinctive cytological features. Asexual reproduction in the formation of monospores, which involves differentiation from vegetative cells, occurs in California populations of several species. Meristematic regions of the thallus in *Porphyra* species give rise to carpospore cells, which develop, according to a diurnal sequence of differentiation, into carposporangia. Ultrastructurally, dictyosome (Golgi) activity in the formation of vesicles, storage products, and extracellular materials are features of sporogenesis.

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Metaphase Chromosome Comparisons in Five Species of Hawaiian *Drosophila*

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Polytene chromosome analyses of Hawaiian *Drosophila* have led to an extensive phylogeny of recently diverged species. In the planitibia subgroup, the finding of homosequential, yet morphologically distinct, species has been the basis for studies that attempt to elucidate the genetic nature of the differences between the species. This study is one such attempt in which metaphase chromosomes are analyzed to find differences in the heterochromatin distribution. This was necessary since polytene chromosomes have no visible heterochromatin and cannot give information about its distribution. Five species from the planitibia subgroup were studied; *D. silvestris*, *D. heteroneura*, *D. differens*, *D. planitibia*, and *D. hemipeza*. A simple method of C-banding was used to study the heterochromatin distribution in the five species.

The results show that all five species have a common karyotype of a telocentric X chromosome, a totally heterochromatic Y chromosome, four pairs of telocentric autosomes, and a pair of microchromosomes. Of the five species, four of them, *Drosophila silvestris*, *D. heteroneura*, *D. differens*, and *D. planitibia*, are homosequential in their poly-

tene chromosome banding patterns while *D. hemipeza* differs from the rest by one fixed inversion on the X chromosome. This study shows all except *D. hemipeza* to have identical C-banding patterns. *Drosophila hemipeza* has a slightly different heterochromatin distribution. The X chromosome has proportionately less heterochromatin and the microchromosomes appear to have more heterochromatin than those of the other four species. The absence of any discernible differences in heterochromatin distribution of the four homosequential, and thus, closely related species suggest that major structural rearrangements of the chromosomes could not have played a role in the most recent speciation events that led to these species.

The difference in the heterochromatin distribution of *Drosophila hemipeza* supports the polytene chromosome based phylogeny which depicts *D. hemipeza* as the most phylogenetically distant of the five species, since one would expect the more distant species to have more differences. The finding of this difference, however, is not sufficient evidence to invoke on it a causal role in the speciation event that led to these five species.

The Effects of Selective Predation on Growth and Competitive Interactions between Two Corals, *Montipora verrucosa* and *Porites compressa*, in Kaneohe Bay, Oahu

EVELYN COX¹⁰

Competition for space among coral species is assumed to be acute in some habitats with high coral cover, such as patch reefs in the northern end of Kaneohe Bay. A series of ex-

periments was designed to evaluate the effects of predation by a selective corallivore, *Chaetodon unimaculatus*, on growth and competitive interactions between two corals, *Montipora verrucosa*, the preferred food, and *Porites compressa*. Test coral colonies of each species were subdivided and glued to concrete blocks, with branches of the two species in contact. The selective corallivore was denied

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access to one of the matched sets by chicken wire cages; the other set was left open to grazing.

Caging had no effect on the vertical growth rate of *Porites compressa*. Caged colonies of *Montipora verrucosa* had a mean vertical growth rate of $9.71 \times 10^{-3} \text{ cm d}^{-1}$, while uncaged colonies had a mean vertical growth rate of $3.92 \times 10^{-3} \text{ cm d}^{-1}$, 40.4 percent of the caged growth rate. In the cages, *M. verrucosa* killed *P. compressa* tissue it contacted, as predicted by laboratory observations. Several uncaged colonies showed a reversal of aggressive

dominance, with *P. compressa* killing branches of *M. verrucosa*. A second experimental series, placed in a habitat free of *Chaetodon unimaculatus*, showed that there was a caging effect on the growth of *M. verrucosa*: the mean vertical growth rate outside of cages was 65.4 percent of the mean vertical growth rate within cages. The caging effect, however, is insufficient to account for the decrease in growth rate of *M. verrucosa* in the presence of predation by the selective corallivore, *C. unimaculatus*.

Sugar Transport by Lobster Hepatopancreatic Brush Border Membrane Vesicles from Whole Tissue and Isolated Absorptive Cells¹¹

RONALD E. DUNN¹²

Epithelial brush border membrane vesicles (BBMV) were made from lobster hepatopancreas using Mg^{2+} precipitation. Alkaline phosphatase and Na/K-ATPase activities in these vesicles were enriched 15.0-fold and 1.0-fold, respectively, compared to the original homogenate activities. Complete vesicular closure was confirmed by electron microscopy. Glucose uptake by these vesicles was stimulated by a transmembrane Na^+ gradient, but not by an identical K^+ gradient. Electrogenicity of Na^+ -dependent glucose transport was confirmed in two ways. First, an anion permeability sequence indicated glucose uptake was stimulated in the following order: $\text{SCN}^- > \text{Cl}^- > \text{gluconate}^- > \text{SO}_4^{2-}$. Second, an outwardly directed, valinomycin-induced, K^+ diffusion potential, rendering the vesicle interior electrically negative, enhanced glucose uptake compared to K^+ -loaded vesicles lacking the ionophore. Glucose influx (15 sec uptake) occurred by a combination of carrier-mediated transfer, illustrating Michaelis-Menten kinetics, and nonsaturat-

ing "apparent diffusion." pH (same on both sides) strongly influenced Na^+ -dependent glucose uptake according to the following sequence: pH 6.0 > 7.4 > 8.0, suggesting a possible role of protons in carrier transport of the sugar.

Absorptive R-cells of the hepatopancreatic epithelium were isolated from other cell types by buoyant density centrifugation. The time course of glucose transport by BBMV formed from these purified R-cells was studied. Sugar uptake by R-cell vesicles closely resembled that displayed by similar preparations from the entire tissue in three critical characteristics: (1) glucose uptake was strongly stimulated by external Na^+ , but not K^+ ; (2) Na^+ -dependent sugar accumulation in vesicles resulted in internal concentrations that transiently exceeded those of the external medium before equilibrium was attained; (3) unidirectional transmembrane glucose transport rates of R-cell BBMV were quantitatively similar to those of the entire organ.

Crustacean hepatopancreatic BBMV show absorptive properties similar to those of mammalian intestine and kidney epithelium. Hepatopancreatic R-cell vesicles illustrate transport characteristics similar to those of the whole tissue, suggesting that this cell type has a major role in glucose absorption.

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Some Preliminary Observations on Coral Recruitment in Kaneohe Bay, Oahu¹³

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Major disturbances such as storms kill or damage corals, creating vacant areas that may be recolonized by coral larvae or by the regrowth of partially damaged corals. Artificial or natural substrata are frequently used to simulate disturbed surfaces in order to study the recruitment of coral larvae and subsequent community development. Localized disturbances such as the effects of fish grazing may modify the communities of corals and other sessile organisms that become established on experimental substrata. Experiments designed to investigate differences in coral recruitment to different shallow water reef habitats were performed in Kaneohe Bay, Oahu.

Seven sites were chosen in Kaneohe Bay that were similar in depth but differed in the amount of coral cover, the species of coral, and the densities of grazing fish present. Hollow concrete blocks (19.5 cm along each side) and dead, sunbleached heads of the branching coral *Porites compressa* (similar in volume to the concrete blocks) were placed at the different sites. Five coral heads were collected from each site after 3 mon and broken up. The number of corals that had recruited to each coral head were then counted. After exposure for 3 and then 6 mon, eight blocks were examined from each site. The number of corals recruiting to each of the four outer and four inner surfaces of the blocks were counted. The blocks were then returned to the field.

Pocillopora damicornis was the only coral that recruited to either the blocks or the coral heads after 3 mon. Two other species of coral,

Cyphastrea ocellina and an ahermatype, *?Culicia* sp., were present on the blocks after 6 mon. No recruitment by the two commonest corals in Kaneohe Bay (*Porites compressa* and *Montipora verrucosa*) was found, although spawning of both species occurred while the blocks were in situ. The mean number of corals recruiting to both the blocks and the coral heads differed significantly between sites. Coral recruitment to the two different types of substratum showed similar trends in abundance at each site. After 3 mon, coral recruitment was highest on Heeia patch reef where territories of the damselfish, *Stegastes fasciolatus*, are common. *Stegastes fasciolatus* actively excludes fish grazers such as scarids and acanthurids. After 6 mon the mean number of corals per block was highest on a windward reef flat where grazing fish are uncommon. The numbers of corals present on the blocks were significantly different after 3 and 6 mon. At all but one site, the Heeia patch reef, the number of corals per block increased between 3 and 6 mon. At most sites the majority of individuals of *Pocillopora damicornis* were found on the inside uppermost surface of the blocks. The ahermatypic coral was only found on the undermost outside surface of blocks.

Although Kaneohe Bay is very protected from wave action, unlike other areas in Hawaii where coral reef community development has been studied, there are parallels between the coral recruitment patterns recorded in this and previous studies in Hawaii. In Kaneohe Bay, *Pocillopora damicornis* was the dominant early colonist. In more wave-exposed areas in Hawaii, another species, *Pocillopora meandrina*, is the most common early colonist. Some corals such as *Montipora verrucosa* have been reported to take about 10 yr to recruit to newly available substrata. It is not clear why *Porites compressa* and *Montipora verrucosa* were not present on the blocks or the coral heads.

¹³ Much of this work was done during the 1983 Coral Reef Biology Course held at the Hawaii Institute of Marine Biology. I acknowledge the support and encouragement of participants in the course as well as my committee, chaired by J. H. Brock.

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Productivity of the Seagrass *Halophila hawaiiiana*

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Seagrasses are among the most important marine primary producers and form vast meadows in shallow waters throughout the world. Little is known about the smaller-leaved seagrasses common to the tropics. This investigation examined the growth dynamics of one of these species, *Halophila hawaiiiana* Doty and Stone, and demonstrated a relatively simple method appropriate for evaluating its biomass and productivity.

Transect samples were taken on a *Halophila* meadow in Kaneohe Bay, Oahu. These samples provided information on total plant biomass and leaf area for an established stand. Laboratory and field experiments were used to determine the growth rates based on the plastochrone interval (the time period between the production of successive leaf pairs). Branching habits were also observed.

It was found that plants grown in culture

exhibit a consistent plastochrone interval of 3 to 4 d. Field growth experiments produced nearly identical results. This suggests that *Halophila* will retain a regular plastochrone interval under varying environmental conditions.

The results of this study indicate that the biomass of a *Halophila* meadow can be estimated from leaf area measurements. The required data are easily collected; leaf numbers in a sample are counted and the leaf area of a subsample is measured by optical planimetry. The rate at which new leaves are produced is estimated by counting the number of terminal buds in the sample and using the plastochrone interval. The resulting information provides a functional growth model from which both biomass and productivity of a *Halophila* meadow can be estimated.

Preliminary Observations Concerning the Abundance and Distribution of Planktonic Coral Larvae in Kaneohe Bay, Oahu

GREGOR HODGSON¹⁶

Little quantitative information is available concerning the abundance and distribution of coral planulae following their release from parent colonies. A plankton sampling technique was designed for the capture of coral planulae. It was based on surface tows using a small, fine-mesh net. More than 250 tows were made along five transects established near the southeast fringing reef of Coconut Island. Time between collection and sorting was minimized and low temperature storage was employed in lieu of chemical fixatives to prevent decomposition of the planulae prior to identification.

More than 100,000 cnidarian larvae, most

of which were scleractinian planulae, were collected and sorted. Twelve different types of cnidarian larvae were differentiated. Two appear to be the zoanthina larvae of the zoanthids *Palythoa vestitus* and *Zoanthus pacificus*. Six were identified as the planulae of the corals *Pocillopora damicornis*, *Porites compressa*, *Montipora verrucosa*, *M. dilitata*, *Cyphastrea ocellina*, and *Fungia scutaria*. Peak recovery of planulae generally occurred 3–7 d after the onset of spawning or planulation.

Limited data on the vertical distribution of three species of coral planulae indicate that they may undertake a diurnal migration similar to that of other demersal plankton. The potential for the export of large numbers of coral planulae from Kaneohe Bay is considered to be high, but whether this export is significant to recruitment on reefs outside the bay remains to be seen.

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Pair Bond Formation and Monogamy in Two Species of Hawaiian Butterflyfishes (Fam. Chaetodontidae)

THOMAS F. HOURIGAN¹⁷

Monogamy is uncommon among animals, and generally occurs when male and female fitness is optimized by both parents providing some parental care. However, other factors must favor the evolution of pair bonds in many fishes.

Broadcast spawning butterflyfishes show no parental care, yet many form long term, apparently monogamous bonds. Among 75 species for which data are available, 77 percent form pair bonds. Based on observations of two species of pair-bonding butterflyfishes in Hawaii, an hypothesis of the adaptive significance of pair bonding in fishes without parental care is proposed. This hypothesis predicts a division of labor in pair-bonded species, such that males provide the majority of territorial defense, allowing females more time to feed, thereby increasing female reproductive output. A series of field experiments were conducted to test these predictions.

Ten male and five female banded butterflyfish, (*Chaetodon multicinctus*) and five female and five male fourspot butterflyfish (*C. quadrimaculatus*) were removed from their respective mates. Changes in territory size, feeding rates, and agonistic encounters were recorded and compared to controls. In both species, solitary females engaged in greatly increased numbers of agonistic encounters, with

an accompanying decrease in territory size and feeding rate. Re-pairing occurred quickly. Increases in territory size and feeding rate by females, however, did not occur until several days after re-pairing, when males began to participate in defense activities. In contrast, solitary males showed no decrease in territory size although agonistic encounters did increase significantly. Feeding rates of males remained the same, or in several cases increased. Additional field manipulations were conducted to investigate male vs. female site tenacity, the effects of resources on mate choice, and to separate the effects of time spent by females in re-pairing from time spent in territorial defense.

These manipulations suggest that pair bonded females receive significant benefits in food resource acquisition. Increased feeding by females is probably translated into increased reproductive output and thereby increased fitness. In addition, individual males are able to defend territories in which these females reside and spawn, suggesting mating exclusivity. Thus pair-bonded males which have exclusive access to these females will also show increased fitness. Thus, this study demonstrates a new mechanism potentially responsible for the evolution of a monogamous social system without parental care.

Patchwork Patchreefs: Clonal Diversity of the Coral *Porites compressa* in Kaneohe Bay, Oahu

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Morphological characteristics were used in conjunction with an immunocompatibility assay to examine the genetic diversity of a patchreef population of *Porites compressa*. Visually identical colonies which exhibited

tissue graft fusion were identified at distances of from 0.2 m to 100 m across the reef. In a 2 m \times 10 m transect of the reef, 49 percent of the 291 colonies of *P. compressa* were identified as belonging to nine morphologically distinct and immunocompatible groups. Three of these morphotypes alone comprised 40 percent of the total *P. compressa* cover within the transect, but were not found on nearby patchreefs where other morphotypes

were predominant. The clonal structure of each patchreef is apparently unique. Sexual recruitment and the genetic diversity of *P. compressa* on mature reefs appear to be low, while asexual reproduction by the establishment of clones derived from fragments appears to be a significant factor resulting in a population dominated by a small number of individual clonal types.

The Development of Auditory Function in the Brain: A Study of Far-Field Evoked Responses in Newborn and Adult Chickens

AKIKO KATAYAMA¹⁹

The development of auditory processing in the brain of the chicken was examined by far-field Auditory evoked Brainstem Response (ABR) averaging. Chickens were used because of their frequent use in embryological studies of the auditory nervous system. In the ABR technique, synchronous activity of neurons in the auditory pathway is evoked by presenting a brief click stimulus, and the response is recorded with large remote electrodes. A computer is used to average 512 or 1024 responses in order to extract the auditory potentials from the ongoing background electroencephalogram (EEG). Separate peaks of electrical activity in the ABR reflect synchronous activation in separate neural elements in the auditory pathway.

In juveniles, a series of ABR peaks was observed within 5 msec after the onset of a stimu-

lus. A similar but more compressed and discrete series of peaks was observed in adult animals. One of the interwave latencies was significantly shorter ($p \leq 0.05$) in adults than it was in juveniles. Among juveniles, that same interwave latency was significantly shorter in 6- and 7-day-old animals than it was in 1- to 3-day-old animals. This suggests that maturation processes, such as the formation of myelin, are occurring during the first week after hatching, and continue in later weeks in at least a part of the central auditory pathway. This physiological evidence for postnatal maturation has recently been complemented by psychophysical studies of auditory sensitivity conducted by Gray and Rubel, who report improvement in high frequency hearing thresholds measured behaviorally as chickens mature during the first postnatal week.

The Supply of Empty Shells and the Population Structure of the Hermit Crab *Calcinus seurati*

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The shell utilization patterns of three intertidal populations of the hermit crab *Calcinus seurati* near Kaneohe Bay, Oahu, were studied. The study sites differed with respect to their physical characteristics, number of gastropods inhabiting the area, and the

availability of empty gastropod shells. The purpose of the study was to test the shell limitation hypothesis which states that shells limit the structure and reproductive dynamics of the hermit crab population.

At the Kaneohe Marine Corps Air Station site there was a small population of the gastropod *Nerita picea*, resulting in a lack of large- and medium-sized empty shells within the habitat. There was a large population of small littorines which provided accessible empty small shells to the hermit crab population. The large population of crabs was dominated by juveniles. Those females that reproduced did so at a small size in a small shell which reduced the clutch size, resulting in a lowered fitness.

At Chinaman's Hat the size of the hermit crab population was limited by the lack of available habitat space. The population of littorines and nerites was large, thus supplying shells of all size classes. The population of hermit crabs was small, but all size classes were

represented. Females were larger, inhabited larger shells, and had larger clutch sizes, resulting in a higher fitness.

Kapapa Island had large populations of both littorines and nerites which provided empty shells of all size classes. During the summer months empty gastropod shells were very abundant in all but the largest size classes. During the winter months there were fewer empty shells. The hermit crab population was large, with significantly larger animals than any of the other study populations, but juveniles were rare. The females had the highest fitness, with large clutch sizes and year-round reproduction.

The hypothesis of shell limitation is supported by the results at two of the study sites. However, the situation at Kapapa Island does not support the hypothesis. Therefore, availability and size of empty shells are neither of universal nor of equal importance to hermit crabs in different environments.

Evidence for Sex Change and Data on Spawning Frequency from the Gonads of a Pomacanthid Fish

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This study was undertaken to test two hypotheses based on behavioral observations of the Caribbean Rock Beauty Angelfish, *Holacanthus tricolor*, Family Pomacanthidae:

1. *H. tricolor* is a protogynous hermaphrodite.

2. *H. tricolor* spawns daily throughout the year.

Seven males (\bar{x} = 155 mm SL; range: 141–163 mm) and 12 females (\bar{x} = 106 mm SL; range: 75–128 mm) were collected at St. Croix, U.S. Virgin Islands, in the morning, at midday, and in the afternoon in May 1981 and September 1982. The gonads were removed and prepared for microscopic examination

using standard histological techniques. Aliquots were taken from the ovaries prior to histological preparation in order to make quantitative estimates of the oocytes present.

Examination of the testes revealed that the vas deferens in all of the males was formed secondarily according to accepted criteria. This characteristic is considered to be evidence of protogynous sex reversal. The testes from the May collection were all larger and contained more mature sperm than did the testes collected in September which suggests seasonal differences in sperm production.

Of the 12 females, 10 had mature ovaries which contained an average 20,000 vitellogenic oocytes/gram ovary (range: 12,000–35,000). Of these 10 ovaries, 8 were hydrating. Ovaries from the morning collec-

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tion contained oocytes in early hydration; ovaries from the midday collection contained oocytes in mid-hydration, and ovaries from the afternoon collection contained oocytes in late hydration. Therefore, *H. tricolor* appears to have a daily hydration schedule.

Mature ovaries collected in May contained an average 5000 hydrating oocytes/gram ovary (range; 4000–6000) while mature ovaries collected in September contained an average 700 hydrating oocytes/gram ovary (range: 0–2000). The two nonhydrating mature ovaries were collected in September and indicate that not all females are spawning daily during this time of year. Furthermore, an average 2700 newly atretic oocytes/gram ovary (range; 2000–3000) were present in all three ovaries which contained less than 500 hydrating oocytes/gram ovary. This suggests that atresia of vitellogenic oocytes before they complete vitellogenesis may be at least par-

tially responsible for the low number of hydrating oocytes in these ovaries.

Two of the 12 females collected did not have mature ovaries. One of these, the smallest female collected (75 mm SL), had an immature ovary containing only gonial and previtellogenic oocytes. The other was the largest female collected (128 mm SL) and had an ovary containing gonial, previtellogenic oocytes, and numerous brown bodies which were believed to be late stage atretic oocytes. This is characteristic of the atresia stage of protogynous sex reversal, and therefore, this ovary is believed to be transitional.

These data support the first hypothesis that *H. tricolor* is a protogynous hermaphrodite. With respect to the second hypothesis, not all females spawn daily in September. Seasonal differences in gamete production occur in both males and females.

Opening of Bivalves by a Nonchelate Crustacean Predator

COLIN J. LAU²²

During a study on crustacean feeding biology, the slipper lobster, *Scyllarides squammosus*, was found to open bivalves of the Families Isognomonidae and Ostreidae in the laboratory. It is notable that members of the Family Scyllaridae lack functional chelae for obtaining food. Two basic attack behaviors were typically displayed. They consisted of:

(1) Wedging—the dactyls of the first pereopods were progressively wedged into the shell opening of the bivalve. Oysters (*Ostrea sandvicensis*) that were cemented to the substrate were often pried open with a rocking motion which allowed the animal to use contractions of the leg muscles in concert with the applied weight of the lobster. Rocking back and forth exhausted the adductor muscle of the oyster and allowed the dactyls of the first pereopod to be wedged in further. Similarly, toothed pearl shells (*Isognomon incisum* and

Isognomon perna) were first removed from the substrate by tearing the attachment of the byssal threads, and then wedged with the first pereopod dactyls while holding onto the pearl shell with the fourth and fifth pereopods. The first walking legs were pressed outward while the second and third pereopods pulled the nearer valve toward the lobster. As the first pereopods were wedged progressively inward, the adductor muscle was usually severed by the dactyl of the second pereopod, and the soft-bodied parts of the mollusk were lifted out and consumed.

(2) Patience attack—an unusual behavior associated with opening of well-attached bivalves (*Ostrea sandvicensis*) was a surprise wedging attack. The dactyls of the first three pairs of pereopods probed the lip of the aperture, and then were held poised centimeters above the opening. After approximately fifteen minutes, the oyster shell re-opened and the lobster quickly and quite suddenly plunged the dactyls of the walking legs into

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the opening, severed the adductor muscles, and removed the soft parts of the prey for consumption.

Evidence of bivalve opening in the field was provided by placing newly caught lobsters in enclosures of a reef with naturally occurring toothed pearl shells and oysters. Data indicate

a preference for the larger toothed pearl shells over the smaller oysters. Feeding observations indicate that bivalves may be a primary component of slipper lobster diets. To date, only *Scyllarides squammosus* has been observed to use such specialized behavior in opening bivalves.

Reproduction in *Galaxaura* (Rhodophyta)

JANE E. LEWIS²³

Galaxaura is a genus of calcareous red algae with tropical and subtropical distribution. This genus is unusual within the phylum Rhodophyta due to the occurrence of dimorphic thalli, where gametophytes and sporophytes are approximately the same size but of different morphologies. While dimorphism has been observed from the field and in herbarium collections, this feature remains to be experimentally confirmed through life history studies. The taxonomy cannot be solved until sporophytes can be paired with the correct gametophytes. This study investigates processes of prefertilization and immediate postfertilization in *Galaxaura* species, and is one in a series of studies elucidating the life history details of *Galaxaura*.

Female plants of *Galaxaura pacifica* and *G. oblongata* were collected at Ala Moana Park and Hau'ula Park, Oahu. Light and scanning electron microscopy were used to observe details of the carpogonial branch, the specialized female reproductive structure, and pre- and postfertilization stages. Transmission electron microscopy was used for detailed cy-

tological studies of reproductive structures. The carpogonial branch of both *Galaxaura pacifica* and *G. oblongata* is an elongate three-celled structure which develops side branchlets before fertilization. The trichogyne, the receptive part of the terminal cell, extends beyond the calcified layers of the thallus, and fertilization is external. During the initial postfertilization stage, diploid branches develop to produce the terminal carpospores, which are diploid reproductive cells. Many carpospores can be produced by the same branch.

Processes of prefertilization and postfertilization are different in the two *Galaxaura* species under investigation. Size and orientation of the reproductive cells are distinguishing characteristics. Developmental morphology of the female reproductive structure is unique for each species. These findings provide an understanding of the sequence of postfertilization events for these *Galaxaura* species, which is essential to an understanding of their life histories.

Intervention Analysis of Power Plant Impact on Fish Populations²⁴

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²⁴ This work was done under the direction of D. J. Jude, University of Michigan, Great Lakes Research Division, Ann Arbor, Michigan.

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Intervention analysis was applied to 10 yr (years 1973–1982) of field fish abundance data at the D. C. Cook Nuclear Power Plant, southeastern Lake Michigan. Three log-transformed catch series, comprising monthly observations, were examined for each com-

bination of two species (alewife, *Alosa pseudoharenga*, or yellow perch, *Perca flavescens*) and gear (trawl or gill net): catch at the plant discharge transect, catch at the reference transect, and the ratio of plant catch to reference catch. Time series with age groups pooled as well as series separated by age groups were examined. Based on intervention analysis, no change in the abundance of fish populations could be attributed to plant operation.

Approximately 15 percent of the series analyzed showed significant serial correlation other than that due to seasonality. Results of analysis of variance, applied to the same series as for the intervention analysis, indicated that the effect of the plant operation on adult yellow perch was significant at $\alpha < 0.055$; the abundance of the adult perch at the reference transect increased relative to perch abundance at the plant transect. The disagreement

between the results of the two statistical techniques could be explained by the presence of substantial serial correlation in the perch series. When the ANOVA procedure was used the serial correlation was not accounted for and therefore the error variance was underestimated. Employment of intervention analysis would insure that detection of any plant-induced change in fish abundance in the vicinity of the power plant was not due to temporally correlated observations.

Additionally, a modification of the intervention analysis technique was applied to investigate trends in abundance at both the plant discharge and reference transects. Significant declines were detected for abundance of alewife adults at both of the transects. Results of the trend analysis support the contention that the alewives have undergone a lake-wide decrease in abundance during the 1970s.

The pH-Dependence of Motility and the Acrosome Reaction of Guinea Pig Spermatozoa²⁶

SUSAN J. MURPHY²⁷

Mammalian spermatozoa must undergo both capacitation and the acrosome reaction before they are capable of fertilizing eggs. Capacitation is a physiological process normally occurring within the female genital tract. The acrosome reaction is always preceded by capacitation and involves membrane vesiculation of a caplike region on the sperm head (the acrosome) with the subsequent release of its contents.

The acrosome reaction is dependent upon the presence of Ca^{2+} in the medium and is influenced by the pH of the medium. Several studies have demonstrated inhibition of the acrosome reaction among sperm populations incubated in media with low pH values. These

studies, however, do not inform us whether the inhibition by low pH is due to the inhibition of the acrosome reaction per se, or the prevention of capacitation preceding the acrosome reaction (or both).

To determine the direct effects of pH on the acrosome reaction, a population of fully capacitated guinea pig spermatozoa, ready for a "synchronous" acrosome reaction, was prepared by incubating the spermatozoa for 1 to 2 h in Ca^{2+} -free modified Tyrodes (mT) medium containing 83 $\mu\text{g}/\text{ml}$ lysophosphatidyl choline (LC). These artificially capacitated spermatozoa were washed twice by centrifugation to remove the LC and then were mixed with samples of Ca^{2+} -containing (2 mM) mT of various pH values (8.2, 7.5, 7.0, 6.7, 6.4, and 6.1) to test for the effects pH might have on the acrosome reaction. After incubation for 15–20 min, each sample was placed on the stage of a microscope with either pseudo-dark-field or phase-contrast optics

²⁶This study was supported by grant no. HD-03402 from the National Institute of Child Health and Human Development.

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($\times 100$), and the overall percentage of motile spermatozoa and the quality of sperm movement were visually estimated. A drop of each suspension was then mounted between a slide and coverslip and examined with a phase-contrast microscope ($\times 450$) for further details of sperm movement and to determine the percentage of acrosome-reacted spermatozoa among at least 100 motile spermatozoa.

Maximum levels of acrosome reaction occurred in media at pH values of 7.5 or 8.2. Acrosome-reacted spermatozoa were vigorously motile. The intensity of sperm motility and the incidence of the acrosome reaction declined with decreasing pH values. At pH 6.1, the motility of all the spermatozoa quickly became very weak. No acrosome reactions occurred at this low pH. The inhibition of motility and acrosome reaction at pH 6.1 was reversed by transferring the spermatozoa back to alkaline medium unless they were exposed to this low pH for longer than 3 h. The inhibition of the acrosome reaction at low pH values (other than 6.1) was counteracted to some extent by increased concentrations of Ca^{2+} (4–10 mM).

Intracellular pH (pH_i) may be partly controlled by the extracellular pH (pH_e), such that when the pH_e is lowered, the pH_i is also lowered. The pH in the mammalian epididymis is generally low and epididymal spermatozoa are generally motionless or only weakly motile. Upon exposure to seminal plasma or media with higher pH values, the spermatozoa become highly motile. This initiation of motility is associated with an efflux of

intracellular H^+ , causing an increase in pH_i , and might be explained by relatively "free" permeability of H^+ through the sperm plasma membrane, such that the pH_i can increase or decrease in response to pH_e .

That the acrosome reaction (and not capacitation) of guinea pig spermatozoa is itself pH-dependent and reversibly inhibited by low pH is supported by similar results from studies using sea urchin spermatozoa, which, unlike mammalian spermatozoa, do not require capacitation prior to the acrosome reaction.

Transferring spermatozoa from an acidic medium containing 2 mM Ca^{2+} to an alkaline medium containing 0 mM Ca^{2+} produced very few acrosome-reacted spermatozoa instead of a population consisting mainly of acrosome-reacted spermatozoa, as would have been expected if Ca^{2+} had penetrated readily into the cells while they were in the low pH medium. Increasing the Ca^{2+} concentration to 4–10 mM slightly counteracted inhibition of the acrosome reaction for sperm samples at pH values of 6.4 and 6.7. Sperm samples at pH 6.1 did not undergo acrosome reactions regardless of the concentration of extracellular Ca^{2+} , indicating that Ca^{2+} entry is severely limited or inhibited at this pH. Because an influx of extracellular Ca^{2+} into spermatozoa through the plasma membrane is an essential preliminary to the acrosome reaction, the failure of Ca^{2+} entry into spermatozoa is likely to be the primary cause of the failure of the acrosome reaction in the acidic medium.

Food Habits of Piscivorous Coral Reef Fishes from the Northwestern Hawaiian Islands²⁸

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²⁸ This project received support from the University of Hawaii Sea Grant College Program, the Hawaii Ocean Management Office, and the Hawaii Cooperative Fishery Research Unit.

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Food habits of piscivorous fishes resident on coral reefs were investigated to determine their trophic roles in the community. This study is part of a 4 yr project by the Hawaii Cooperative Fishery Research Unit on the trophic structure of inshore reef fish commu-

nities in the Northwestern Hawaiian Islands. Reef study sites were established at Midway and French Frigate Shoals (FFS) lagoons. Fishes were collected throughout the year and at various locations. Analysis of gut contents was used to determine the degree of piscivory exhibited by each species. Of 112 species analyzed, 36 species representing 17 families showed some evidence of fish consumption, although only 14 species are considered to be primarily piscivorous.

The total number of potential prey fishes and their relative proportions at the Midway and FFS study sites were estimated from visual censuses and various collections, including complete collections made with rotenone of isolated patch reef communities. Of 29 families observed or collected, 24 occurred in the pooled guts of all the resident piscivores analyzed. Goatfishes (Mullidae) accounted for over 22 percent of the total volume of prey and more than 10 percent of the total number. Wrasses (Labridae), parrotfishes (Scaridae), gobies (Gobiidae), surgeonfishes (Acanthuridae), cardinalfishes (Apogonidae), and squirrelfishes (Holocentridae) each accounted for more than 10 percent of either the total number or volume of prey. Although butterflyfishes (Chaetodontidae) were totally lacking in the guts of piscivores, they accounted for more than 3 percent of the total weight and

2 percent of the total number of fishes from four complete community collections.

Proportions of the various prey taxa in the community of potential prey fishes were compared with proportions encountered in the pooled guts of all the piscivores analyzed. Goatfishes (primarily *Mulloid* spp.), the dominant prey group, typically occurred on visual censuses as large transient schools passing over a reef or sheltering there briefly. They were not represented in large numbers in the various collecting efforts. Occurrence of other species of transient prey in the guts of piscivores suggests that resident piscivores rely on nonresident prey to some degree. Data from gut analyses indicate that young recruits to a reef are preyed upon heavily by otherwise nonpiscivorous carnivores as well as by resident piscivores. Two sympatric lizardfishes (*Synodus ulae* and *Saurida gracilis*), the most highly piscivorous species observed, were analyzed for evidence of partitioning of food resources. These species were common on study sites and may account for a major portion of resident fish mortality. A low degree of dietary overlap of prey families was observed between these two species. Data and field observations suggest that these piscivores separate feeding niches spatially rather than temporally. Such partitioning patterns may serve to reduce competition if prey are a limiting resource.

Expression of a SRC-Homologous Gene during Embryogenesis of the Hawaiian Sea Urchin, *Tripneustes Gratilla*³⁰

THOMAS C. RAYSON³¹

Cellular proto-oncogenes, homologous to retroviral transforming genes, have been detected in many vertebrates but few invertebrates. Although the function of these proto-oncogenes in normal cells is not yet known,

reports of the developmentally regulated expression of some of these genes in vertebrates suggests that they may have a role in normal cellular development. This report describes our studies of the expression of the putative *c-src* proto-oncogene in the developing sea urchin embryo model system.

Cellular lysates of whole sea urchin embryos at various stages were examined by immunological and enzymatic assay for the protein product encoded by a *src*-homologous

³⁰ This research was supported by grants from the National Cancer Institute and the University of Hawaii Research and Training Revolving Fund to Alan F. Lau.

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gene. Tumor-bearing rabbit (TBR) sera reactive to the avian sarcoma virus pp60^{v-src} protein was used in immunoprecipitations to identify the putative sea urchin *c-src* protein by its specific *in vitro* phosphorylation of the anti-*src* antibody using γ -[³²P]-ATP as the phosphate donor.

[³²P]-labeled immunoglobulin heavy chain (Ig-H) from the anti-*src* serum was readily identified on SDS-polyacrylamide gels while control, nonimmune serum showed no phosphorylation. High voltage electrophoresis on thin layer cellulose of acid-hydrolyzed, [³²P]-labeled Ig-H extracted from gel bands demonstrated that the phosphorylation occurred on a tyrosine residue characteristic of vertebrate *c-src* kinase activity. Expression of this tyrosine-specific protein kinase activity was developmentally regulated. It was highest in eggs, decreased approximately fivefold through blastula stage and then subsequently increased threefold to the 56 h pluteus stage. Immunoprecipitation of a sea urchin protein

by anti-*src* TBR serum was demonstrated directly using [³⁵S]-methionine-labeled cell lysates. A band of apparent molecular weight of 54,000 daltons was specifically precipitated by the immune serum. Since the mobility of this band was not affected by protease inhibitors present in the immunoprecipitation, the putative *c-src* protein from sea urchin appears to be smaller than the typical 60,000 dalton *c-src* protein isolated from vertebrates. Finally, immunoprecipitation of [³²P]-labeled sea urchin lysates with anti-*src* serum indicated that the 54,000 dalton protein was phosphorylated similar to vertebrate *c-src* proteins.

These results add to the short list of cellular proto-oncogenes, their protein products and activities which have been identified in invertebrate tissues. The observation of expression and developmental regulation of a cellular proto-oncogene during sea urchin embryogenesis suggests that studies in this model system may help elucidate the normal cellular function of proto-oncogenes.

A Taxonomic Survey of Microscopic Freshwater Algae in Hawaii: A Report on Some Common Species³²

VERNON T. SATO³³

Growth and succession in natural phytoplankton populations are influenced by seasonal changes. Recent laboratory studies have demonstrated the existence of allelopathic factors which may influence the growth of other organisms. Because these interactions may be important in aquatic ecological studies, it is necessary that the microscopic organisms be taxonomically defined beyond their biochemical characteristics.

A survey of freshwater, brackish, and marine habitats has revealed the presence of

more than 600 species of microscopic algae in Hawaii. When combined with those from the existing literature, well over 1000 taxa are represented in aquatic and edaphic habitats. Approximately 45 percent of these occur in freshwater. This report presents the results of a survey of freshwater microscopic algae, focusing on about twenty of the more common species.

Water samples from various freshwater sources on Kauai, Oahu, Maui, and Hawaii were examined by light microscopy and enrichment culture methods. Fresh material was observed by light microscopy or fixed in preservative when microscopes were not immediately available. The observed organisms were identified to species whenever possible. Pure cultures of rare species or other interesting organisms were isolated from field material on

³² The author wishes to acknowledge the assistance of personnel at the Hawaii Anuenue Fisheries Research Center and at the University of Hawaii, Department of Botany for providing facilities and supplies used during this study.

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agar and transferred to liquid cultures enriched with Bold's Basal Medium.

In descending order, ponds were observed to be dominated by green algae (Phylum: Chlorophyta), bluegreens (Phylum: Cyanophyta), and diatoms (Phylum: Bacillariophyta). Adjacent ponds often have very different phytoplankton populations. In many cases there appears to be a codominance of organisms. There are persistent species which may be present throughout the year and occasionally become dominant. Others may never become dominant and are observed for only short periods of time. Some species may appear as the dominant organism for several months, while others dominate for less than a

month. In streams, tufts of epilithic algae may provide habitats where unattached microscopic forms may grow. The epipellic flora consists of a number of species of diatoms as well as bluegreens and certain desmids.

Phytoplanktonic succession is influenced by seasonal factors. The effects of such factors, however, may be more difficult to define in subtropical areas, such as Hawaii, than in temperate areas. The potential of allelopathic factors in influencing the species composition of a community cannot be ignored. Such interactions may be as important as seasonality in determining domination and succession in microalgal populations.

Alternate Male Reproductive Strategies in the Giant Malaysian Prawn, *Macrobrachium rosenbergii*³⁴

TERESA M. TELECKY³⁵

Equivalent-aged males of the giant Malaysian prawn, *Macrobrachium rosenbergii*, cultured under identical conditions, show a bimodal size distribution. Larger males, termed "bulls," have proportionately longer chelipeds than females; these are used antagonistically both intra- and interspecifically and in precopulatory display. Smaller males, termed "runts," have chelipeds which are proportionately similar to those of females. Runts have been considered to be nonreproductive members of a "sire pool" since they may develop into bulls when removed from the presence of bulls. The proximate causes of this male polymorphism include visual or tactile cues, while the ultimate causes remain unknown. This study demonstrates the significance of polymorphism in male reproductive

competition in culture populations of *M. rosenbergii*.

Copulation in *Macrobrachium rosenbergii* follows the precopulatory molt of the female. After the molt, the bull exhibits extensive precopulatory behaviors followed by overturning the female for a ventral-ventral copulation. Members of groups of runts were observed to obtain apparent copulatory access to females associated with bulls. In typical observations, a bull is distracted by a group of runts and a single runt may sneak copulation with the female. The reproductive behavior of runts was different than that of bulls and is probably related to their smaller size. Rather than overturning the female for copulation, runts slip their ventral surface beneath that of the female. Runts were paired with females in isolation to determine their fertilization capability; all pairs produced viable embryos.

To determine the relative reproductive success of runts, two populations were constructed using animals of known genotypes. Genotypes were determined from muscle tissue examined at the glutamate-oxaloacetate transaminase locus, which is polymorphic in

³⁴This study was completed as a requirement for the degree of Master of Science from the University of Nevada, Department of Biology. It was supported in full by grants awarded to Robert E. L. Taylor, University of Nevada, Department of Veterinary Medicine, Reno, Nevada.

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Macrobrachium rosenbergii. The populations were composed of bulls, runts, and females in proportions similar to those observed in culture. During a 3 mon period, the number of matings per runt as determined by analysis of clutch genotypes was significantly less than that of bulls. However, runts contributed 11–34 percent of observed matings.

The production and maintenance of female-attracting features, such as the large body size and chelipeds of bulls, is probably costly and males should be selected to deceive females when possible. In species where a large variation in male physical attributes

exists, alternate reproductive strategies are predicted. Males of many species utilize small size to gain reproductive access to females by intercepting them when they become attracted to the qualities of a large displaying male. The runts of *Macrobrachium rosenbergii* may be the result of selection for such a strategy, although it is unknown whether natural populations exhibit male polymorphism. In cultured populations where there are few bulls and many females, runts may profit from this alternate reproductive strategy, and it may prove difficult to artificially select against such a trait.